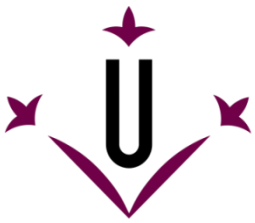


Title: Climatic controls of decomposition drive the global biogeography of forest tree symbioses

Authors: Steidinger BS[1]*, Crowther TW[2]†*, Liang J†[3,4]*, Van Nuland ME[1], Werner GDA[5], Reich PB[6,7], Nabuurs G[8], de-Miguel S[9,10], Zhou M[3], Picard N[11], Herault B[12], Zhao X[4], Zhang C[4], Routh D[2] Abegg, Meinrad; Adou Yao, C. Yves; Alberti, Giorgio; Almeyda Zambrano, Angelica; Alvarez-Davila, Esteban; Alvarez-Loayza, Patricia; Alves, Luciana F.; Ammer, Christian; Antón-Fernández, Clara; Araujo-Murakami, Alejandro; Arroyo, Luzmila; Avitabile, Valerio; *Aymard, Gerardo; Baker, Timothy; Bałazy, Radomir; Banki, Olaf; Barroso, Jorcely; Bastian,* Meredith; Bastin, Jean-Francois; Birigazzi, Luca; Birnbaum, Philippe; Bitariho, Robert; Boeckx, Pascal; Bongers, Frans; Bouriaud, Olivier; Brancalion, Pedro H. S.; Brandl, Susanne; Brearley, Francis Q.; Brienen, Roel; Broadbent, Eben; Bruelheide, Helge; Bussotti, Filippo; Cazzolla Gatti, Roberto; Cesar, Ricardo; Cesljar, Goran; Chazdon, Robin; Chen, Han Y. H.; Chisholm, Chelsea; Cienciala, Emil; Clark, Connie J.; Clark, David; Colletta, Gabriel; Condit, Richard; Coomes, David; Cornejo Valverde, Fernando; Corral-Rivas, Jose J.; Crim, Philip; Cumming, Jonathan; Dayanandan, Selvadurai; de Gasper, André L.; Decuyper, Mathieu; Derroire, Géraldine; DeVries, Ben; Djordjevic, Ilija; Iêda, Amaral; Dourdain, Aurélie; Obiang, Nestor Laurier Engone; Enquist, Brian; Eyre, Teresa; Fandohan, Adandé Belarmain; Fayle, Tom M.; Feldpausch, Ted R.; Finér, Leena; Fischer, Markus; Fletcher, Christine; Fridman, Jonas; Frizzera, Lorenzo; Gamarra, Javier G. P.; Gianelle, Damiano; Glick, Henry B.; Harris, David; Hector, Andrew; Hemp, Andreas; Hengeveld, Geerten; Herbohn, John; Herold, Martin; Hillers, Annika; Honorio Coronado, Eurídice N.; Huber, Markus; Hui, Cang; Cho, Hyunkook; Ibanez, Thomas; Jung, Ilbin; Imai, Nobuo; Jagodzinski, Andrzej M.; Jaroszewicz, Bogdan; Johannsen, Vivian; Joly, Carlos A.; Jucker, Tommaso; Karminov, Viktor; Kartawinata, Kuswata; Kearsley, Elizabeth; Kenfack, David; Kennard, Deborah; Kepfer-Rojas, Sebastian; Keppel, Gunnar; Khan, Mohammed Latif; Killeen, Timothy; Kim, Hyun Seok; Kitayama, Kanehiro; Köhl, Michael; Korjus, Henn; Kraxner, Florian; Laarmann, Diana; Lang, Mait; Lewis, Simon; Lu, Huicui; Lukina, Natalia; Maitner, Brian; Malhi, Yadvinder; Marcon, Eric; Marimon, Beatriz Schwantes; Marimon-Junior, Ben Hur; Marshall, Andrew Robert; Martin, Emanuel; Martynenko, Olga; Meave, Jorge A.; Melo-Cruz, Omar; Mendoza, Casimiro; Merow, Cory; Monteagudo Mendoza, Abel; Moreno, Vanessa; Mukul, Sharif A.; Mundhenk, Philip; Nava-Miranda, Maria G.; Neill, David; Neldner, Victor; Nevenic, Radovan; Ngugi, Michael; Niklaus, Pascal; Oleksyn, Jacek; Ontikov, Petr; Ortiz-Malavasi, Edgar; Pan, Yude; Paquette, Alain; Parada-Gutierrez, Alexander; Parfenova, Elena; Park, Minjee; Parren, Marc; Parthasarathy, Narayanaswamy; Peri, Pablo L.; Pfautsch, Sebastian; Phillips, Oliver; Piedade, Maria Teresa; Piotto, Daniel; Pitman, Nigel C. A.; Polo, Irina; Poorter, Lourens; Poulsen, Axel Dalberg; Poulsen, John R.; Pretzsch, Hans; Ramirez Arevalo, Freddy; Restrepo-Correa, Zorayda; Rodeghiero, Mirco; Rolim, Samir; Roopsind, Anand; Rovero, Francesco; Rutishauser, Ervan; Saikia, Purabi; Saner, Philippe; Schall, Peter; Schelhaas, Mart-Jan; Schepaschenko, Dmitry; Scherer-Lorenzen, Michael; Schmid, Bernhard; Schöngart, Jochen; Searle, Eric; Seben, Vladimír; Serra-Diaz, Josep M.; Salas-Eljatib, Christian; Sheil, Douglas; Shvidenko, Anatoly; Silva-Espejo, Javier; Silveira, Marcos; Singh, James; Sist, Plinio; Slik, Ferry; Sonké, Bonaventure; Souza, Alexandre F.; *Stereńczak, Krzysztof; Svenning, Jens*-Christian; Svoboda, Miroslav; Targhetta, Natalia; Tchebakova, Nadja; Steege, Hans ter; Thomas, Raquel; Tikhonova, Elena; Umunay, Peter; Usoltsev, Vladimir; Valladares, Fernando; van der Plas, Fons; Van Do, Tran; Vasquez Martinez, Rodolfo; Verbeeck, Hans; Viana, Helder; Vieira,

Simone; von Gadow, Klaus; Wang, Hua-Feng; Watson, James; Westerlund, Bertil; Wiser, Susan; Wittmann, Florian; Wortel, Verginia; Zagt, Roderick; Zawila-Niedzwiecki, Tomasz; Zhu, Zhi-Xin; Zo-Bi, Irie Casimirand Peay KG[1]†

Affiliations:
[1] Department of Biology, Stanford University, Stanford CA USA
[2] Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland
[3] Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA
[4] Research Center of Forest Management Engineering of State Forestry Administration, Beijing Forestry University, Beijing, China
[5] Department of Zoology, University of Oxford, Oxford UK
[6] Department of Forest Resources, University of Minnesota
[7] Hawkesbury Institute for the Environment, Western Sydney University
[8] Wageningen University and Research
[9] Departament de Producció Vegetal i Ciència Forestal, Universitat de Lleida-Agrotecnio Center
[10] Forest Science and Technology Centre of Catalonia (CTFC)
[11] Food and Agriculture Organization of the United Nations
[12] Cirad, INP-HB, Univ Montpellier, UPR Forêts et Sociétés

*These authors contributed equally to this work and share the first-author
†Corresponding authors: Email kpeay@stanford.edu; albeca.liang@gmail.com; tom.crowther@usys.ethz.ch

The identity of the dominant microbial symbionts in a forest determines the ability of trees to access limiting nutrients from atmospheric or soil pools[1,2], sequester carbon[3,4] and withstand the impacts of climate change[1-7]. Characterizing the global distribution of symbioses, and identifying the factors that control it, are thus integral to understanding present and future forest ecosystem functioning. Here we generate the first spatially explicit map of forest symbiotic status using a global database of 1.2 million forest inventory plots with over 28,000 tree species. Our analyses indicate that climatic variables, and in particular climatically-controlled variation in decomposition rate, are the primary drivers of the global distribution of major symbioses. We estimate that ectomycorrhizal (EM) trees, which represent only 2% of all plant species[8], constitute approximately 60% of tree stems on Earth. EM symbiosis dominates forests where seasonally cold and dry

climates inhibit decomposition, and are the predominant symbiosis at high latitudes and elevation. In contrast, arbuscular mycorrhizal (AM) trees dominate aseasonally warm tropical forests and occur with EM trees in temperate biomes where seasonally warm-and-wet climates enhance decomposition. Continental transitions between AM and EM dominated forests occur relatively abruptly along climate driven decomposition gradients, which is likely caused by positive plant-microbe feedbacks. Symbiotic N-fixers, which are insensitive to climatic controls on decomposition compared with mycorrhizal fungi, are most abundant in arid biomes with alkaline soils and high maximum temperatures. The climatically driven global symbiosis gradient we document represents the first spatially-explicit, quantitative understanding of microbial symbioses at the global scale and demonstrates the critical role of microbial mutualisms in shaping the distribution of plant species.

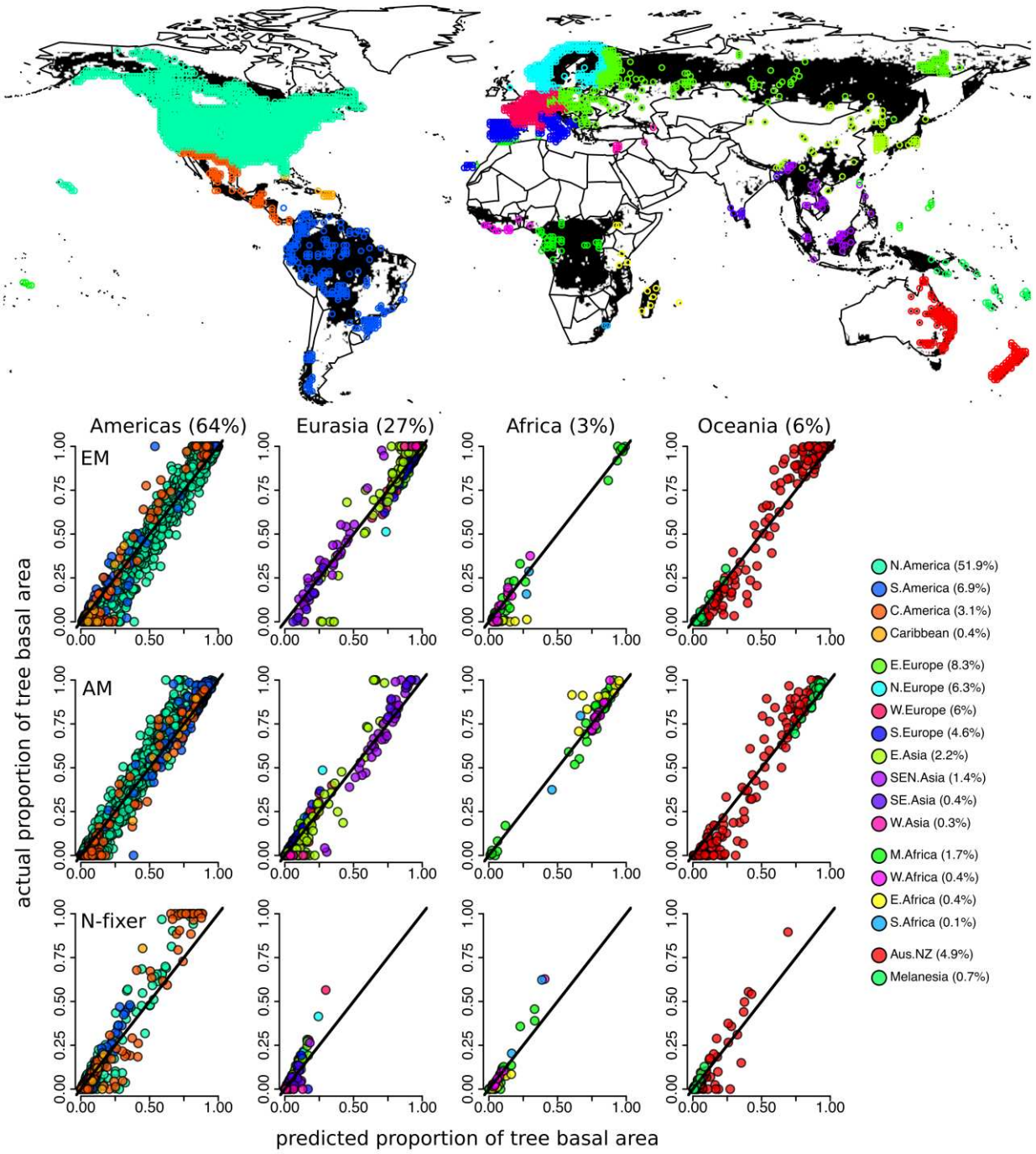
Microbial symbionts strongly influence the functioning of forest ecosystems. They exploit inorganic, organic[2] and/or atmospheric forms of nutrients that enable plant growth[1], determine how trees respond to elevated CO_2[6], regulate the respiratory activity of soil microbes[3,9], and affect plant species diversity by altering the strength of conspecific negative density dependence[10]. Despite growing recognition of the importance of root symbioses for forest functioning[1,6,11] and the potential to integrate symbiotic status into Earth system models that predict functional changes to the terrestrial biosphere[11,12], we lack spatially-explicit, quantitative maps of the different root symbioses at the global scale. Generating these quantitative maps of tree symbiotic states would link the biogeography of functional traits of belowground microbial symbionts with their 1.5 trillion host trees[13], spread across Earth's forests, woodlands, and savannas.

104 The dominant guilds of tree root symbionts, arbuscular mycorrhizal (AM) fungi,
105 ectomycorrhizal (EM) fungi, ericoid mycorrhizal (ErM) fungi, and nitrogen (N)-fixing bacteria
106 (N-fixer) are all based on the exchange of plant photosynthate for limiting macronutrients. The
107 AM symbiosis is the oldest of the four, having evolved nearly 500 million years ago, with EM,
108 ErM and N-fixer plant taxa having evolved multiple times from an AM basal state. Plants that
109 form the AM symbiosis are markedly more diverse than the other symbiotic groups, comprising
110 nearly 80% of all terrestrial plant species, and principally rely on AM fungi for enhancing
111 mineral phosphorus (P) uptake[14]. EM fungi evolved more recently from saprotrophic ancestors,
112 and as a result may be better than AM fungi at competing with free living soil microbes for
113 resources[3]. As such, some EM fungal lineages are more capable of mobilizing organic sources of
114 soil nutrients (particularly nitrogen) compared with AM fungi[15,16]. Association with EM fungi,
115 but not AM fungi, has been shown to allow trees to accelerate photosynthesis in response to
116 increased atmospheric CO_2 when soil nitrogen (N) is limiting[6] and to inhibit soil respiration by
117 decomposer microbes[3,9] (but see [17]). Because increased plant photosynthesis and decreased soil
118 respiration both reduce atmospheric CO_2 concentrations, the EM symbiosis is associated with
119 buffering the Earth's climate against anthropogenic changes.
120 In contrast to mycorrhizal fungi, which extract nutrients from the soil, symbiotic N-fixers
121 (Rhizobia and Actinobacteria) convert atmospheric N_2 to plant-usable forms. Symbiotic N-fixers
122 are responsible for a large fraction of biological soil-N inputs, which can increase N-availability
123 in forests where they are locally abundant[18]. Both N-fixing bacteria and EM fungi often demand
124 more plant photosynthate than does the AM symbiosis[14,19,20]. Because tree growth and
125 reproduction are limited by access to inorganic, organic and atmospheric sources of N, the
126 distribution of these root symbioses is likely to reflect both environmental conditions that

maximize the cost-benefit ratio of symbiotic exchange as well as physiological constraints on different symbionts.

In one of the earliest efforts to understand the functional biogeography of plant root symbioses, Sir David Read[21] categorically classified biomes by their perceived dominant mycorrhizal type and hypothesized that seasonal climates favor hosts associating with EM fungi due to their ability to compete directly for organic N. By contrast, it has been proposed that sensitivity to low temperatures has prevented N-fixers from dominating outside the tropics, despite the potential for N-fixation to alleviate N-limitation in boreal forests[20,22]. However, global scale tests of these proposed biogeographic patterns and their proposed climate drivers are lacking or inconclusive[23-25] and we have no understanding of the regional variations in this proposed latitudinal trend. To address this research gap, we compiled the first global ground-sourced survey database to reveal numerical abundances of each symbiosis across the global forested biomes, rather than incidence (presence or absence, e.g.,[23-25]), which is essential for identifying the shapes and potential mechanisms underlying transitions in forest symbiotic state along climatic gradients[26,27].

We determined the abundance of tree symbioses using GFBi, an extension from the plot-based Global Forest Biodiversity (GFB[28]) database, which contains over 1.2 million forest inventory plots of individual-based measurement records from which we derive abundance information for entire tree communities (Figure 1).



146

147 **Figure 1. A map of 1 by 1 degree grid cells where we analyzed the proportion of tree stems**
148 **and basal area for different symbiotic guilds (above). Circles show the location of training**
149 **data, colored by geographic origin, while black squares show the extent of model**
150 **projections. Panels below the map show actual vs. predicted proportion of basal area for**
151 **ectomycorrhizal (EM), arbuscular mycorrhizal (AM), and N-fixer trees by continent and**
152 **subregion, and demonstrate globally consistent model performance.**

153 Using published literature on the evolutionary histories of mycorrhizal and N-fixer
154 symbioses[8,25,29-33], we assigned plant species from the GFBi to one of 5 symbiotic guilds: AM,
155 EM, ErM, N-fixer, and non- or weakly-mycorrhizal (NM). Most plants with symbioses derived
156 from the AM state retain the genetic potential to associate with AM fungi[14]. Thus, consistent
157 with other studies in this field[29], we assigned tree species to the AM-exclusive guild if they were
158 not EM, ericoid mycorrhizal, non-mycorrhizal, or N-fixers. While there is some uncertainty in
159 such assignments, direct investigation of mycorrhizal status when done supports this
160 assumption[34]. Because individual measurements of mycorrhizal colonization are not possible at
161 this scale, our models represent potential symbiotic associations.

162 To identify the key factors structuring symbiotic distributions we assembled 70 global
163 predictor layers: 19 climatic (annual, monthly, and quarterly temperature and precipitation
164 variables), 14 soil chemical (total soil N density, microbial N, C:N ratios and soil P fractions,
165 pH, cation exchange capacity), 5 soil physical (soil texture and bulk density), 26 vegetative
166 indices (leaf area index, total stem density, enhanced vegetation index means and variances), and
167 5 topographic variables (elevation, hillshade) (Table S7). Because decomposition is the dominant
168 process by which soil nutrients become available to plants, we generated 5 additional layers that
169 estimate the climatic control of decomposition. We parameterized decomposition coefficients
170 according to the Yasso07 model[35,36] using the following equation:
171

$$k = \mathrm{Exp}(0.095T_i - 0.00014\,T_i^2)\,(1-\mathrm{Exp}[\,-1.21\,P_i]), \qquad (1)$$

172 where P_i and T_i are precipitation and mean temperature, either quarterly or annually, and the
173 constants 0.0095 ($=\beta_1$) $=$0.00014 ($=\beta_2$) , and -1.21 ($=\gamma$) are parameters fit using a previous global
174 study of leaf litter mass-loss[36]. Although local decomposition rates can vary significantly based
175 on litter quality or microbial community composition[37], climate is the primary control at the

176 global scale[36]. Decomposition coefficients describe how fast different chemical pools of leaf
177 litter lose mass over time relative to a parameter, α, that accounts for leaf-chemistry.
178 Decomposition coefficients (k) with values of 0.5 and 2 indicate a halving and doubling of
179 decomposition rates relative to α, respectively (Supplemental Materials).

180 Given the large set of possible environmental predictors, we used the random forest
181 machine-learning algorithm to identify the best predictors of global symbiosis distributions. The
182 random forest algorithm averages multiple regression trees, each of which uses a random subset
183 of all the model variables to predict a response. These regression trees identify optimal values
184 along a predictor-gradient to "split" the model response into different nodes (e.g., predictions
185 could be "split" into nodes of 50 or 75% of EM basal area depending on whether mean annual
186 temperature is > or < 20°C). We ranked the importance of each variable according to inc node
187 purity, which measures the decrease in model error that occurs whenever the response is split on
188 that variable (Figure 2ABC). We first determined the influence and relationship of all 75
189 predictor layers on forest symbiotic state and then optimized our models using a stepwise
190 reduction in variables, from least- to most-important. Soil chemical, vegetative, and topographic
191 variables were the first to be eliminated from our models in this way. In a subsequent model that
192 included only layers of climate, decomposition, and certain soil physical and chemical
193 information, we found that the 4 most important variables accounted for >85% of the explained
194 variability. We plot the partial-fits of these four variables for each symbiotic guild (Figure
195 2ABC).

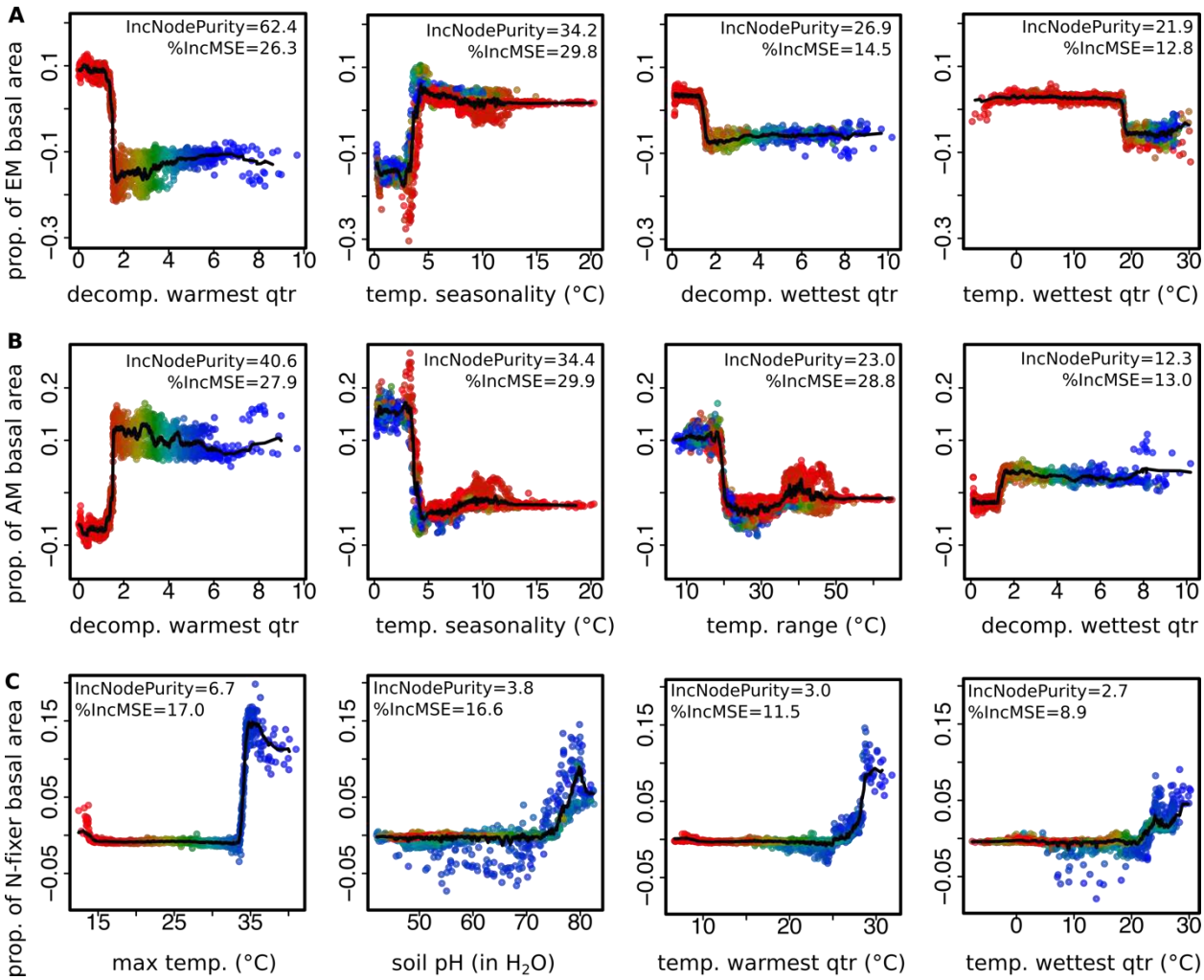


Figure 2. Partial plots of residual variation explained by the four most important predictors of the proportion of tree basal area belonging to the (A) ectomycorrhizal (EM), (B) arbuscular mycorrhizal (AM), and (C) N-fixer symbiotic guilds. Variables are listed in declining importance from left to right, as determined by inc node purity, with points colored with a red-green-blue gradient according to their position on the x-axis of the most important variable (left-most panels for each guild), allowing cross visualization between predictors. Each panel lists two measures of variable importance, inc node purity (used for sorting) and %IncMSE (see Supplemental Information for description). Decomposition rates in (A) and (B) are in units of leaf litter mass loss per quarter. The abundance of each symbiont type transitions sharply along climatic gradients, suggesting that sites near the threshold are particularly vulnerable to switching their dominant symbiont guild with climate changes.

The three most numerically abundant tree symbiotic guilds each have reliable environmental signatures, with the four most important predictors accounting for 81, 79, and 52% of the total variability in EM, AM, and N-fixer relative basal area, respectively. Models for

ErM and NM lack strong predictive power given the relative rarity of these symbiotic states amongst trees, although the raw data do identify some local abundance hotspots for ErM (Figure S1). As a result, we focus the remainder of results and discussion on the three major tree symbiotic states (EM, AM, N-fixer). Despite the fact that data from N. and S. America constitute 65% of the training data (at the 1 by 1 degree grid scale), our models accurately predict the proportional abundances of the three major symbioses across all major geographic regions (Figure 1). The high performance of our models, which is robust to both K-fold cross-validation and rarefying samples so that all continents are represented with equal depth (Figures S10-12), suggest that regional variations in climate (including indirect effects on decomposition) and soil pH (for N-fixers) are the primary factors influencing the relative dominance of each guild at the global scale (geographic origin only explained ~2-5% of the variability in residual relative abundance) (Figure 1BCD, Table S8).

Random forest models should not be projected across predictor gradients that fall outside the ranges of their training data (e.g., grid cells with higher mean annual temperatures than the maximum used to fit the models). To prevent the over-projecting of our models over pixels where we lacked training data, we subset a global grid of predictor layers depending on whether (1) the grid cell fell within the top 60% of land surface with respect to tree stem density[13] and either (2) fell within the univariate distribution of all the predictor layers from our training data and/or (3) fell within an 8-dimensional hypervolume defined by the unique set of the 4-best predictors of the relative abundance of each guild (Figure 2, Supplemental Materials). We then projected our models across only those grid cells that met these criteria, which constitutes 46% of the global land surface and 88% of global tree stems (Figure 1; Figure S16). While model validation indicates that our projections are robust, additional ground truthing of predictions to

identify any discrepancies would be incredibly valuable. If such discrepancies exist they can help fine tune climate-symbiosis models, or identify areas where climate might favors invasion by symbioses that have not yet evolved or dispersed to a particular biogeographic region.

In contrast to a recent global analysis of root traits, which concluded that plant evolution has favored reduced dependence on mycorrhizal fungi[38], we find that trees associating with the relatively more C-demanding and recently-derived EM fungi[14,19] represent the dominant tree-symbiosis. By taking the average proportion of EM trees, weighted by spatially-explicit global predictions for tree stem density[13], we estimate that approximately 60% of trees on earth are EM, despite the fact that only 2% of plant species associate with EM fungi (vs. 80% associating with AM fungi)[8,29]. Outside of the tropics, the estimate for EM relative abundance increases to approximately 80% of trees.

Turnover among the major symbiotic guilds results in a tri-modal latitudinal abundance gradient, with the proportion of EM trees increasing (and AM trees decreasing) with distance from the equator, while N-fixing trees reach peak abundance in the arid zone around 30 degrees (Figure 3A, Figure 4). These trends are driven by abrupt transitional regions along continental climatic gradients (Figure 2), which skew the distribution of symbioses among biomes (Figure 3A) and drive strong patterns across geographic and topographic features that influence climate. For example, moving north or south from the equator, the first transitional zone separates warm (aseasonal), AM-dominated, tropical broadleaf forests (>75% median basal area, vs. 8% for EM trees) from the rest of the EM-dominated world forest system (Figure 2AB; Figure 3A). It stretches longitudinally across 25 degrees N and S, just beyond the dry tropical broadleaf forests (with 25% EM tree basal area; Figure 3A), where average monthly temperature variation reaches 3-5°C (Figure 2AB).

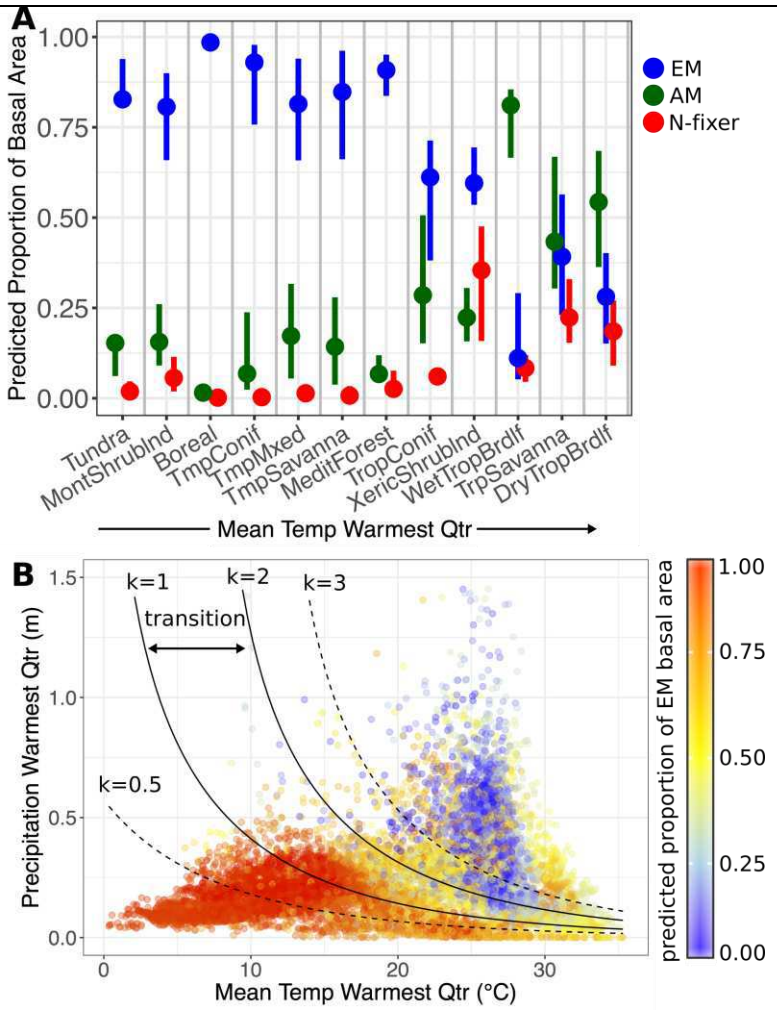


Figure 3. (A) The median proportion of tree basal area per biome (arranged in order of increasing mean temperature of the warmest quarter) for ectomycorrhizal (EM), arbuscular mycorrhizal (AM), and N-fixer symbiotic guilds. EM trees dominate all extra-tropical biomes. (B) The dependency of decomposition coefficients (k, solid and dotted lines) on temperature and precipitation during the warmest quarter with respect to predicted dominance of mycorrhizal symbiosis. AM forests transition to EM forests abruptly in the region between k=1 and 2, which is consistent with positive feedback between climatic and biological controls of decomposition.

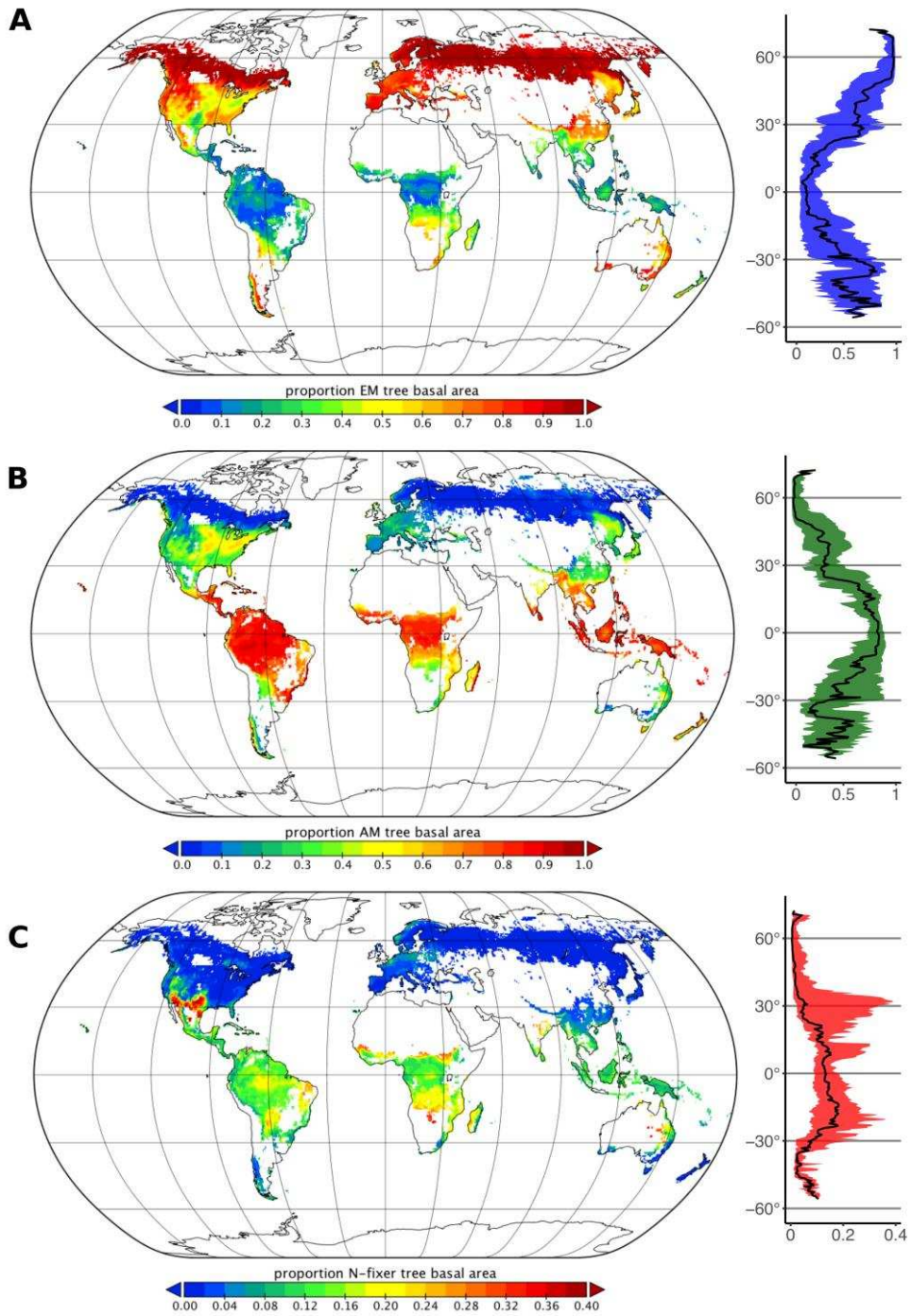
Moving further N or S, the second transitional climate zone separates regions where decomposition coefficients during the warmest quarter of the year are less than 2 (see Figure 3B for the associated temperature and precipitation ranges). In N. America and China, this transition zone spans longitudinally around 50 degrees N, separating the mixed AM / EM temperate forests from their neighboring EM dominated boreal forests (75 vs 100% EM tree basal area, respectively; Figure 3A). This transitional decomposition zone bypasses W. Europe, which has temperature seasonality > 5°C, but lacks sufficiently wet summers to accelerate decomposition coefficients beyond values associated with mixed AM/EM forests. The latitudinal transitions in symbiotic state observed among biomes are mirrored by within-biome transitions along elevation

gradients. For example, in tropical Mexico, warm and wet quarter decomposition coefficients < 2 occur along the slopes of the Sierra Madre, where mixed AM-exclusive and N-fixer woodlands in arid climates transition to EM dominated tropical coniferous forests (75% basal area, Figure 3A, Figure 4ABC, Figure S17-19). The southern hemisphere, which lacks the landmass to support extensive boreal forests, experiences a similar latitudinal transition in decomposition rates along the ecotone separating its tropical and temperate biomes, around 28 degrees S.

The abrupt transitions that we detected between forest symbiotic states along environmental gradients suggest that positive feedbacks may exist between climatic and biological controls of decomposition[11,36]. In contrast to AM fungi, some EM fungi can use oxidative enzymes to mineralize organic nutrients from leaf litter, converting nutrients to plant-usable forms before transferring them to their host trees[2,5]. Relative to AM trees, the leaf litter of EM trees is also chemically more resistant to decomposition, with higher C:N ratios and higher concentrations of decomposition-inhibiting secondary compounds[11]. Thus, EM leaf litter can exacerbate climatic barriers to decomposition, promoting conditions where EM fungi have superior nutrient-acquiring abilities to AM-fungi[5,11]. Such positive-feedbacks are known to cause abrupt ecosystem transitions along smooth environmental gradients between woodlands and grasses: trees suppress fires, which promotes seedling recruitment, while grass fuels fires, which kill tree seedlings[39]. Our study provides the first evidence that rapid transitions in tree community structure along climate gradients could also be governed by positive-feedbacks between symbiotic guilds and nutrient cycling; although other types of interactions, such as environmentally sensitive competition hierarchies among symbiotic guilds, could also lead to abrupt transitions without specifically invoking feedback effects. In either case, the existence of abrupt transitions suggests that trees and associated microbial symbionts in transitional regions

290 along decomposition gradients should be susceptible to drastic turnover in symbiotic state with
291 future environmental changes[40].

292 To illustrate the sensitivity of global patterns of tree symbiosis to climate change, we use
293 the climate relationships we developed for current climate to project potential changes due to
294 climate change. Relative to our global predictions using the most recent climate data, model
295 predictions using the projected climates for 2070 suggest the abundance of EM trees will decline
296 by as much as 10% (using a relative concentration pathway of 8.5 W/m^2; Figure S25). Due to
297 their position along decomposition gradients relative to the abrupt shift from EM to AM forests
298 (Figure 2AB), our models predict the largest declines in EM abundance will occur along the
299 boreal-temperate ecotone, although declines in species abundances can lag decades, or even
300 centuries or millennia, behind associated climatic changes[41]. The predicted decline in EM trees
301 corroborates the results of common garden transfer and simulated warming experiments, which
302 demonstrate that some important EM hosts will decline at the boreal-temperate ecotone in altered
303 climates[42-44]. Because of the low tree diversity in boreal forests, tree species loss around
304 transition zones may have major consequences for forest related economic activity[45].
305
306



307

308 **Figure 4. Predicted global maps (left) and latitudinal gradients (right, with solid line**
309 **indicating the median and colored ribbon spanning the range from the 5% and 95%**
310 **quantiles) of the proportion of tree basal area for (A) ectomycorrhizal (EM), (B)**
311 **arbuscular mycorrhizal (AM), and (C) N-fixer symbiotic guilds.**
312

313 The change in dominant nutrient exchange symbioses along climate gradients highlights
314 the interconnection between atmospheric and soil compartments of the biosphere. The transition
315 from AM to EM dominance corresponds with a shift from P to N limitation of plant growth with
316 increasing latitude[46-48]. Including published global projections of total soil N or P, microbial N,
317 or soil P fractions (labile, occluded, organic, and apatite) did not increase the amount of variation
318 explained by the model or alter the variables identified as most important, and thus were dropped
319 from our analysis. However, this does not necessarily mean that soil nutrient availability is
320 unimportant at the global scale, as the best-available global data likely do not adequately
321 represent local nutrient availability[49,50]. Rather, our finding that climatic controls of
322 decomposition best predict the dominant mycorrhizal associations mechanistically links
323 symbiont physiology with climatic controls of soil nutrient release from leaf litter. These
324 findings are consistent with Read's hypothesis[21] that slow decomposition at high latitudes favors
325 EM fungi due to their increased capacity to liberate organic nutrients[2]. Thus, while more
326 experiments are necessary to understand the specific mechanism by which nutrient competition
327 favors dominance of AM or EM symbioses[26], we propose that the latitudinal and elevational
328 transitions from AM to EM dominated forests be called Read's Rule.
329 While our analyses focus on prediction at large spatial scales appropriate to the available
330 data, our findings with respect to Read's Rule also provide insight into how soil factors structure
331 the fine-scale distributions of tree symbioses within our grid cells. For example, while at a coarse
332 scale we find that EM trees are relatively rare in many wet tropical forests, individual tropical
333 sites in our raw data span the full range from 0 – 100 % EM basal area. In much of the wet
334 tropics, these EM dominated sites exist as outliers within a matrix of predominantly AM trees. In
335 an apparent exception that proves Read's Rule, in aseasonal warm neotropical climates, which

accelerate leaf-decomposition and promote regional AM dominance (Figure 3), EM dominated tree stands can develop in sites where poor soils and recalcitrant litter slow decomposition and N mineralization[26,51]. Landscape-scale variation in the relative abundance of symbiotic states also changes along climate gradients, with variability highest in xeric and temperate biomes (Figure S2), suggesting that the potential of local nutrient variability to favor particular symbioses is contingent on climate.

Whereas EM trees are associated with ecosystems where plant growth is thought to be primarily N-limited, N-fixer trees are not. Our results highlight the global extent of the "N-cycling paradox," wherein some metrics suggest that N-limitation is greater in the temperate zone[46-48], yet N-fixing trees are relatively more common in the tropics[20,52,53] (Figure 3A). We find that N-fixers, which we estimate represent 7% of all trees, dominate forests with annual max temperatures >35°C and alkaline soils (particularly in North America and Africa, Figure 2C). They have the highest relative abundance in xeric shrublands (24%), tropical savannas (21%), and dry broadleaf forest biomes (20%), but are nearly absent from boreal forests (<1%) (Figure 3A, Figure 4). The decline in N-fixer tree abundance we observed with increasing latitude is also associated with a previously documented latitudinal shift in the identity of N-fixing microbes, from facultative N-fixing rhizobial bacteria in tropical forests to obligate N-fixing actinorhizal bacteria in temperate forests[52]. Our data are not capable of fully disentangling the several hypotheses that have been proposed to reconcile the N-cycling paradox[20,54]. However, our results are consistent with the model prediction[22] and regional empirical evidence[27,55,56] that N-fixing trees are particularly important in arid biomes. Based primarily on the observed positive, nonlinear association of N-fixer relative abundance with the mean temperature of the hottest

month (Figure 2C), our models predict a two-fold increase in N-fixer relative abundance when transitioning from humid to dry tropical forest biomes (Figure 3A).

Although soil microbes are a dominant component of forests, both in terms of diversity and ecosystem functioning[5,6,11], identifying global-scale microbial biogeographic patterns remains an ongoing research priority. Our analyses confirm that Read's Rule, which is one of the first proposed biogeographic rules specific to microbial symbioses, successfully describes global transitions between mycorrhizal guilds. More generally, climate driven turnover among the major plant-microbe symbioses represents a fundamental biological pattern in the Earth system, as forests transition from low-latitude arbuscular mycorrhizal, to N-fixer, to high-latitude ectomycorrhizal ecosystems. The predictions of our model (which we make available as a global raster layer) can now be used to represent these critical ecosystem variations in global biogeochemical models used to predict climate-biogeochemical feedbacks within and between trees, soils, and the atmosphere. Additionally, the layer containing the proportion abundance of N-fixing trees can be used to map potential symbiotic N-fixation, which links together atmospheric pools of C and N. Future work can extend our findings to incorporate multiple plant growth forms and non-forested biomes, where similar patterns likely exist, to generate a complete global perspective. Our predictive maps leverage the most comprehensive global forest dataset to generate the first quantitative global map of forest tree symbioses, demonstrating how nutritional mutualisms are coupled with the global distribution of plant communities.

Acknowledgments

This work is supported in part by the Key Project of National Key Research and Development Plan, China (2017YFC0504005); the new faculty start-up grant, Department of Forestry and Natural Resources, Purdue University; Dept. of Energy (DOE) Biological and Environmental

Research Program Early Career Research Grant DE-SC0016097; DOB Ecology, Plant-for-the-Planet and the German Ministry for Economic Development and Cooperation; São Paulo Research Foundation, #2014/14503-7; São Paulo Research Foundation (FAPESP), #2003/12595-7; Proyecto FONACIT No. 1998003436 and UNELLEZ No. 23198105; EU, Sumforest – REFORM, Risk Resiliant Forest Management, FKZ: 2816ERA02S; U.S. National Science Foundation Long-Term Ecological Research grant DEB-1234162, German Science Foundation (DFG), KROOF Tree and stand-level growth reactions on drought in mixed versus pure forests of Norway spruce and European beech, PR 292/12-1; Bavarian State Ministry for Food, Agriculture and Forestry, W07 longterm yield experiments, 7831-26625-2017 and Project No E33; The Deutsche Forschungsgemeinschaft (DFG) Priority Program 1374 Biodiversity Exploratories; The International Tropical Timber Organization, ITTO-Project PD 53/00 Rev.3 (F); The State Forest Management Centre, Estonia, and the Environmental Investment Centre, Estonia; Natural Sciences and Engineering Research Council of Canada Discover Grant Project (RGPIN-2014-04181 and STPGP428641); European Structural Funds by FEDER 2014-2020 GY0006894; European Investment Funds by FEDER/COMPETE/POCI-Operational Competitiveness and Internationalization Programme, under Project POCI-01-0145-FEDER-006958 and National Funds by FCT - Portuguese Foundation for Science and Technology, under the project UID/AGR/04033/2013; Vietnam National Foundation for Science and Technology Development (NAFOSTED-106-NN.06-2016.10); German Research Foundation (DFG, FOR 1246); The project LIFE+ ForBioSensing PL Comprehensive monitoring of stand dynamics in Bialowieza Forest co-funded by Life Plus (contract number LIFE13 ENV/PL/000048) and the National Fund for Environmental Protection and Water Management in Poland (contract number 485/2014/WN10/OP-NM-LF/D); National Natural Scientific Foundation of China (31660055

404 and 31660074); The Polish State Forests National Forest Holding (2016); The Dutch Ministry of
405 Economic Affairs for funding the Dutch National Forest Inventory; The Grant 11-TE11-0100
406 from the U.S. National Space and Aeronautics Administration; the Tropical Ecology,
407 Assessment, and Monitoring (TEAM) / Conservation International project for funding the data
408 collection, and the National Institut Research Amazon (INPA); The Ministère des Forêts, de la
409 Faune et des Parcs du Québec (Canada); The Exploratory plots of FunDivEUROPE received
410 funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant
411 agreement 265171; DBT, Govt. of India through the project 'Mapping and quantitative
412 assessment of geographic distribution and population status of plant resources of Eastern
413 Himalayan region' (sanction order No. BT/PR7928/NDB/52/9/2006 dated 29th September 2006);
414 The financial support from Natural Sciences and Engineering Research Council of Canada to S.
415 Dayanandan; Czech Science Foundation Standard Grant (16-09427S) and European Research
416 Council advanced grant (669609); RFBR #16-05-00496; The project implementation
417 Demonstration object on the transformation of declining spruce forests into ecologically more
418 stable multifunctional ecosystems, ITMS 26220220026, supported by the Research &
419 Development Operational Program funded by the ERDF; The Swedish NFI, Department of
420 Forest Resource Management, Swedish University of Agricultural Sciences SLU; The National
421 Research Foundation (NRF) of South Africa (89967 and 109244) and the South African
422 Research Chair Initiative; University Research Committee of the University of the South Pacific,
423 and New Colombo Plan Funding through the Department of Foreign Affairs and Trade of the
424 Australian government; The TEAM project in Uganda supported by the Moore foundation and
425 Buffett Foundation through Conservation International (CI) and Wildlife Conservation Society
426 (WCS); COBIMFO project funded by the Belgian Science Policy Office (Belspo), contract no.

427 SD/AR/01A; The German Federal Ministry of Education and Research (BMBF) under Grant
428 FKZ 01LL0908AD for the project “Land Use and Climate Change Interactions in the Vu Gia
429 Thu Bon River Basin, Central Vietnam” (LUCCI); Programme Tropenbos Côte d'Ivoire : projet
430 04/97-1111a du “Complément d’Inventaire de la Flore dans le Parc National de Taï”; The Danish
431 Council for Independent Research | Natural Sciences (TREECHANGE, grant 6108-00078B to
432 JCS) and VILLUM FONDEN (grant 16549); ERC Advanced Grant 291585 (“T-FORCES”) and
433 a Royal Society-Wolfson Research Merit Award; RAINFOR plots supported by the Gordon and
434 Betty Moore Foundation and the U.K. Natural Environment Research Council (NERC), notably
435 NERC Consortium Grants ‘AMAZONICA’ (NE/F005806/1), ‘TROBIT’ (NE/D005590/1), and
436 ‘BIO-RED’ (NE/N012542/1); Fundação de Amparo à Pesquisa e Inovação de Santa Catarina,
437 FAPESC (2016TR2524), Conselho Nacional de Desenvolvimento Científico e Tecnológico,
438 CNPq [312075/2013-8); “Investissement d’Avenir” grant managed by Agence Nationale de la
439 Recherche (CEBA, ref. ANR- 10-LABX-25-01); CIFOR's Global Comparative Study on
440 REDD+ funded by the Norwegian Agency for Development Cooperation (Norad), the Australian
441 Department of Foreign Affairs and Trade (DFAT), the European Union (EU), the International
442 Climate Initiative (IKI) of the German Federal Ministry for the Environment, Nature
443 Conservation, Building and Nuclear Safety (BMUB), and the CGIAR Research Program on
444 Forests, Trees and Agroforestry (CRP-FTA), and donors to the CGIAR Fund; The Nature and
445 Biodiversity Conservation Union (NABU) under the project entitled “Biodiversity under Climate
446 Change: Community Based Conservation, Management and Development Concepts for the Wild
447 Coffee Forests”, funded by the German Federal Ministry for the Environment, Nature
448 Conservation and Nuclear Safety (BMU) through the International Climate Initiative (IKI); The
449 Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq); The institutional

project “EXTEMIT - K”, no. CZ.02.1.01/0.0/0.0/15_003/0000433 financed by OP RDE; EC DG VIII grant BZ-5041 (ECOSYN), NWO-WOTRO (W84-204), and GTZ; AfriTRON network plots funded by the local communities and NERC, ERC, European Union, Royal Society and Leverhume Trust; BOLFOR (Proyecto de Manejo Forestal Sostenible- Bolivia); The Global Environment Research Fund F-071 and D-1006, and JSPS KAKENHI Grant Numbers JP17K15289; The National Institute of Biology(Now Research Center for Biology), LIPI (Indonesian Institute of Sciences), Indonesia IFBN project (contract 4000114425/15/NL/FF/gp) funded by ESA; NSF grant DBI-1565046; Swiss National Science Foundation (SNSF No. 130720, 147092); Projects D/9170/07, D/018222/08, D/023225/09 and D/032548/10 funded by the Spanish Agency for International Development Cooperation [Agencia Española de Cooperación Internacional para el Desarrollo (AECID)] and Fundación Biodiversidad, in cooperation with the Universidad Mayor de San Simón (UMSS), the FOMABO (Manejo Forestal en las Tierras Tropicales de Bolivia) project and CIMAL (Compañía Industrial Maderera Ltda.); The Agency for Economic and Environmental Development (DDEE) of the north province of New Caledonia (the projects Ecofor & Cogefor, 2011-2016); Russian Science Foundation (16-17-10284 “The accumulation of carbon in forest soils and forest succession status”); Norwegian Ministry of Food and Agriculture; A grant from the Royal Society and the Natural Environment Research Council (UK) to S.L.L.; The Spanish Agency for International Development Cooperation [Agencia Española de Cooperación Internacional para el Desarrollo (AECID)] and Fundación Biodiversidad, in cooperation with the governments of Syria and Lebanon; COBIMFO Project, Federal Science Policy, Belgium; Consejo Nacional de Ciencia y Tecnología, Mexico; Comisión Nacional Forestla, Mexico; BEF-China project (FOR 891) funded by the German Research Foundation (DFG); WWF Russell Train Fellowship to P.M.U.

(Grant ST54); Wildlife Conservation Society DRC Program under CARPE Funding; Seoul National University Big Data Institute through the Data Science Research Project 2016, R&D Program for Forest Science Technology (Project No. 2013069C10-1719-AA03 & S111215L020110) funded by Korea Forest Service (Korea Forestry Promotion Institute); The European Union's Horizon 2020 research and innovation program within the framework of the MultiFUNGtionality Marie Skłodowska-Curie Individual Fellowship (IF-EF) under grant agreement 655815; Tropenbos International-Suriname; The Institute for World Forestry, University of Hamburg; REMBIOFOR Project "Remote sensing based assessment of woody biomass and carbon storage in forests" funded by The National Centre for Research and Development, Warsaw, Poland, under the BIOSTRATEG program (agreement no. BIOSTRATEG1/267755/4/NCBR/2015); The National Science Centre, Poland (Grant: 2011/02/A/NZ9/00108); Project "Environmental and genetic factors affecting productivity of forest ecosystems on forest and post-industrial habitats" (2011-2015; no. OR/2717/3/11); Project "Carbon balance of the major forest-forming tree species in Poland" (2007-2011; no. 1/07) funded by the General Directorate of State Forests, Warsaw, Poland; and the research professorship for "Ecosystem-based sustainable development" funded by Eberswalde University for Sustainable Development. GK was supported by an Alexander von Humboldt fellowship. GDAW was supported from a Newton International Fellowship from the Royal Society.

We thank the following agencies, initiatives, teams, and individuals for data collection and other technical support: the Global Forest Biodiversity Initiative (GFBI) for establishing the data standards and collaborative framework; United States Department of Agriculture, Forest Service, Forest Inventory and Analysis (FIA) Program; University of Alaska Fairbanks; The SODEFOR,

Ivory Coast; the Queensland Herbarium and past Queensland Government Forestry and Natural Resource Management Departments and staff for data collection for over seven decades. Ziaur Rahman Laskar, Salam Dilip, Bijit, Bironjoy and Samar; Badru Mugerwa and Emmanuel Akampurira, together with a team of field assistants (Valentine and Lawrence); all persons who made the Third Spanish Forest Inventory possible, especially the main coordinator, J. A. Villanueva (IFN3); Italian and Friuli Venezia Giulia Forest Services (Italy); Rafael Ávila and Sharon van Tuylen, Insituto Nacional de Bosques (INAB), Guatemala for facilitating Guatemalan data; The National Focal Center for Forest condition monitoring of Serbia (NFC), Institute of Forestry, Belgrade, Serbia; The Thünen Institute of Forest Ecosystems (Germany) for providing National Forest Inventory data; All TEAM data provided by the Tropical Ecology Assessment and Monitoring (TEAM) Network, a collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution, and the Wildlife Conservation Society, and partially funded by these institutions, the Gordon and Betty Moore Foundation, and other donors, with thanks to all current and previous TEAM site manager and other collaborators that helped collecting data; The people of the Redi Doti, Pierrekondre and Cassipora village who were instrumental in assisting with the collection of data and sharing local knowledge of their forest; and the dedicated members of the field crew of Kabo 2012 census. Yadvinder Malhi's contribution was supported by an ERC Advanced Investigator Award GEM-TRAITS (321131).

References

1 Batterman, S. A. et al. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. Nature **502**, 224-227, doi:10.1038/nature12525 (2013).

2 Shah, F. et al. Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. New Phytol **209**, 1705-1719, doi:10.1111/nph.13722 (2016).

3 Averill, C., Turner, B. L. & Finzi, A. C. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. Nature **505**, 543-+, doi:10.1038/nature12901 (2014).

4 Clemmensen, K. E. et al. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science **339**, 1615-1618, doi:10.1126/science.1231923 (2013).

5 Cheeke, T. E. et al. Dominant mycorrhizal association of trees alters carbon and nutrient cycling by selecting for microbial groups with distinct enzyme function. New Phytol. **214**, 432-442, doi:10.1111/nph.14343 (2017).

6 Terrer, C., Vicca, S., Hungate, B. A., Phillips, R. P. & Prentice, I. C. Mycorrhizal association as a primary control of the CO2 fertilization effect. Science **353**, 72-74, doi:10.1126/science.aaf4610 (2016).

7 Johnson, D. J., Beaulieu, W. T., Bever, J. D. & Clay, K. Conspecific negative density dependence and forest diversity. Science **336**, 904,Äì907 (2012).

8 Brundrett, M. C. in Biogeography of Mycorrhizal Symbiosis 533-556 (Springer, 2017).

9 Averill, C. & Hawkes, C. V. Ectomycorrhizal fungi slow soil carbon cycling. Ecol Lett **19**, 937-947, doi:10.1111/ele.12631 (2016).

10 Bennett, J. A. et al. Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. Science **355**, 181-184 (2017).

11 Phillips, R. P., Brzostek, E. & Midgley, M. G. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. New Phytol. **199**, 41-51, doi:10.1111/nph.12221 (2013).

12 Oleson, K. W. et al. Technical description of version 4.0 of the Community Land Model (CLM). (2010).

13 Crowther, T. W. et al. Mapping tree density at a global scale. Nature **525**, 201 (2015).

14 Heijden, M. G., Martin, F. M., Selosse, M. A. & Sanders, I. R. Mycorrhizal ecology and evolution: the past, the present, and the future. New Phytol. **205**, 1406-1423 (2015).

15 Lindahl, B. D. & Tunlid, A. Ectomycorrhizal fungi–potential organic matter decomposers, yet not saprotrophs. New Phytol. **205**, 1443-1447 (2015).

16 Liu, X. et al. Partitioning of soil phosphorus among arbuscular and ectomycorrhizal trees in tropical and subtropical forests. Ecol Lett **21**, 713-723 (2018).

17 Zhu, K., McCormack, M. L., Lankau, R. A., Egan, J. F. & Wurzburger, N. Association of ectomycorrhizal trees with high carbon-to-nitrogen ratio soils across temperate forests is driven by smaller nitrogen not larger carbon stocks. Journal of Ecology **106**, 524-535 (2018).

18 Binkley, D., Sollins, P., Bell, R., Sachs, D. & Myrold, D. Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology **73**, 2022-2033 (1992).

19 Leake, J. et al. Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. Canadian Journal of Botany **82**, 1016-1045 (2004).

20 Hedin, L. O., Brookshire, E. N. J., Menge, D. N. L. & Barron, A. R. in Annual Review of Ecology Evolution and Systematics Vol. 40 Annual Review of Ecology Evolution and Systematics 613-635 (Annual Reviews, 2009).

21 Read, D. J. Mycorrhizas in Ecosystems. Experientia **47**, 376-391, doi:Doi 10.1007/Bf01972080 (1991).

22 Houlton, B. Z., Wang, Y.-P., Vitousek, P. M. & Field, C. B. A unifying framework for dinitrogen fixation in the terrestrial biosphere. Nature **454**, 327 (2008).
23 Bueno, C. G. et al. Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. Global Ecology and Biogeography **26**, 690-699 (2017).
24 Soudzilovskaia, N. A., Vaessen, S., van't Zelfde, M. & Raes, N. in Biogeography of Mycorrhizal Symbiosis 223-235 (Springer, 2017).
25 Brundrett, M. C. & Tedersoo, L. Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol. (2018).
26 Peay, K. G. The mutualistic niche: mycorrhizal symbiosis and community dynamics. Annual Review of Ecology, Evolution, and Systematics **47**, 143-164 (2016).
27 Pellegrini, A. F., Staver, A. C., Hedin, L. O., Charles-Dominique, T. & Tourgee, A. Aridity, not fire, favors nitrogen-fixing plants across tropical savanna and forest biomes. Ecology **97**, 2177-2183 (2016).
28 Liang, J. et al. Positive biodiversity-productivity relationship predominant in global forests. Science **354**, aaf8957 (2016).
29 Brundrett, M. C. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant and Soil **320**, 37-77, doi:10.1007/s11104-008-9877-9 (2009).
30 Werner, G. D., Cornwell, W. K., Cornelissen, J. H. & Kiers, E. T. Evolutionary signals of symbiotic persistence in the legume–rhizobia mutualism. Proceedings of the National Academy of Sciences **112**, 10262-10269 (2015).
31 Afkhami, M. E. et al. Symbioses with nitrogen-fixing bacteria: nodulation and phylogenetic data across legume genera. Ecology **99**, 502-502 (2018).
32 Tedersoo, L. et al. Global database of plants with root-symbiotic nitrogen fixation: Nod DB. Journal of Vegetation Science (2018).
33 Wang, B. & Qiu, Y.-L. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza **16**, 299-363 (2006).
34 McGuire, K. et al. Dual mycorrhizal colonization of forest-dominating tropical trees and the mycorrhizal status of non-dominant tree and liana species. Mycorrhiza **18**, 217-222 (2008).
35 Palosuo, T., Liski, J., Trofymow, J. & Titus, B. Litter decomposition affected by climate and litter quality—testing the Yasso model with litterbag data from the Canadian intersite decomposition experiment. Ecological Modelling **189**, 183-198 (2005).
36 Tuomi, M. et al. Leaf litter decomposition—estimates of global variability based on Yasso07 model. Ecological Modelling **220**, 3362-3371 (2009).
37 Bradford, M. A. et al. Climate fails to predict wood decomposition at regional scales. Nature Climate Change **4**, 625 (2014).
38 Ma, Z. et al. Evolutionary history resolves global organization of root functional traits. Nature (2018).
39 Staver, A. C., Archibald, S. & Levin, S. Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. Ecology **92**, 1063-1072 (2011).
40 Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems. Nature **413**, 591 (2001).

41 Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**, 37 (2003).
42 Reich, P. B. & Oleksyn, J. Climate warming will reduce growth and survival of Scots pine except in the far north. Ecol Lett **11**, 588-597, doi:10.1111/j.1461-0248.2008.01172.x (2008).
43 Fernandez, C. W. & Kennedy, P. G. Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? New Phytol. **209**, 1382-1394, doi:10.1111/nph.13648 (2016).
44 Reich, P. B. et al. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nature Climate Change **5**, 148 (2015).
45 Hanewinkel, M. & Peyron, J.-L. Tackling climate change—the contribution of scientific knowledge in forestry. Ann Forest Sci **71**, 113-115 (2014).
46 Vitousek, P. M. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology **65**, 285-298 (1984).
47 McGroddy, M. E., Daufresne, T. & Hedin, L. O. Scaling of C: N: P stoichiometry in forests worldwide: Implications of terrestrial redfield-type ratios. Ecology **85**, 2390-2401 (2004).
48 Reich, P. B. & Oleksyn, J. Global patterns of plant leaf N and P in relation to temperature and latitude. Proceedings of the National Academy of Sciences of the United States of America **101**, 11001-11006 (2004).
49 Vitousek, P. M. & Sanford Jr, R. L. Nutrient cycling in moist tropical forest. Annu Rev Ecol Syst **17**, 137-167 (1986).
50 Grunwald, S., Thompson, J. & Boettinger, J. Digital soil mapping and modeling at continental scales: Finding solutions for global issues. Soil Science Society of America Journal **75**, 1201-1213 (2011).
51 Corrales, A., Mangan, S. A., Turner, B. L. & Dalling, J. W. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. Ecol Lett **19**, 383-392, doi:10.1111/ele.12570 (2016).
52 Menge, D. N., Lichstein, J. W. & Ángeles-Pérez, G. Nitrogen fixation strategies can explain the latitudinal shift in nitrogen-fixing tree abundance. Ecology **95**, 2236-2245 (2014).
53 Ter Steege, H. et al. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature **443**, 444 (2006).
54 Menge, D. N. et al. Why are nitrogen-fixing trees rare at higher compared to lower latitudes? Ecology **98**, 3127-3140 (2017).
55 Liao, W., Menge, D. N., Lichstein, J. W. & Ángeles-Pérez, G. Global climate change will increase the abundance of symbiotic nitrogen-fixing trees in much of North America. Global Change Biol (2017).
56 Gei, M. et al. Legume abundance along successional and rainfall gradients in Neotropical forests. Nature ecology & evolution, 1 (2018).